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PERIOD LENGTH IN CYCLIC ANIMAL POPULATIONS

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Abstract. Although cyclic animal dynamics have long been a focus of scientific interest, the variable cycle lengths are poorly understood. Based on a review of the literature, we suggest that period length in animals showing multiannual cycles is related to the life span of their food plant rather than to any trait of the animal, such as mass or fecundity. We envisage that this pattern is brought about by a prolonged mobilization of induced defenses in longer lived plants, which can better afford periods of low reproductive output than can short-lived plants. On the basis of this hypothesis we expect animals with similar diets to show similar cycle lengths, irrespective of taxonomy and size. A path analysis, on the vertebrate herbivores, shows that 92% of the variation in cycle length is explained by food-plant longevity and that body mass adds little to this.

Key words: *bird; cyclic herbivore populations; food-plant longevity; herbivory; insect; mammals; multiannual cycles; plant life span.*

INTRODUCTION

In the hope of finding general principles in population dynamics, scientists have long taken an interest in species with cyclic population fluctuations. Apart from trying to find the factor(s) causing delayed density dependence that can produce cyclicity, efforts have been focused on periodicity in cycles, varying between three and more than 30 years. Attempts to explain cycle intervals have concentrated on maternal effects (insects; Ginzburg and Tanneyhill 1994), population growth rate (May 1981), and in vertebrates, body mass (Calder 1983). The logic behind these views is that fast-growing populations of small animals will pass through their cycles faster than slow-growing populations of large species, whatever the factor(s) causing the population change (Ginzburg and Tanneyhill 1995). Calder (1983) suggested that cycle length for herbivores, but not for predators, which presumably follow the cycle of their prey, is associated with the intrinsic rate of population increase (r), which scales with the 4th root of body mass. Peterson et al. (1984) found a very good fit between cycle length and body mass (exponent 0.26) in 41 species of herbivorous birds and mammals. However, the inclusion of a larger sample of herbivores decreased both the fit and the scaling exponent (Krukonis and Schaffer 1991), who also asked (p. 471) ''If carnivores simply tag along after their food supply, why not herbivores after theirs?''

We explored this latter suggestion by assuming that traits of food plants rather than those of the herbivores determine cycle length, as a consequence of costs and benefits linked with grazing-induced delayed plant resistance (Haukioja and Hakala 1975, Rhoades 1985). For such resistance to drive multi-annual cycles it is required that grazed plants show a delayed response by increasing defense substances/structures and that the relaxation of this response in the absence of grazing should take several years. These conditions were analyzed by Underwood (1999) in a mathematical model. For most plant species examined in this study (Tables 1 and 2) induced resistance has been shown (Karban and Baldwin 1997: Table 4.1), but information on relaxation periods is sparse. However, indirect evidence for long-lasting effects of induced resistance has been found: Haukioja and Neuvonen (1987) recorded significant reductions in fecundity of the moth *Epirrita autumnata* feeding on birches *Betula pubescens* defoliated up to four years earlier; Bryant et al. (1991) found a reduced palatability for snowshoe hares (*Lepus americanus*) in twigs of trees browsed three to four years earlier; and Baltensweiler (1985) reported an increased mortality level in larch bud moth *Zeiraphera diniana* caterpillars for several years following an outbreak. The benefit of an induced defense for the plant is a reduced grazing pressure, often for many years, which is balanced against its cost, a reduction in growth and seed production (Karban and Baldwin 1997). We suggest that short-lived plants demobilize their induced defenses sooner than long-lived plants, because the latter can better withstand lost growth and reproduction. In other words, one lost reproductive event, or part of it, constitutes a smaller fraction of the reproductive value of a long-lived plant compared to a short-lived plant, tipping the cost–benefit balance in favor of a longer-lasting defense period for long-lived plants. Therefore, cycles of herbivores that graze on trees will be longer than cycles of those grazing on herbs, irrespective of taxonomic affiliation, size of the herbivore,

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TABLE 1. Life history and cycle length of vertebrate herbivores and longevity of their food plants.

Herbivore	Data source	Cycle length, median (yr)	Body mass (kg)	Plant species	Plant longevity, mean (yr)
Lagopus scoticus	Watson and Moss (1979)	6	0.6	*Calluna vulgaris*	25
Lagopus lagopus	Andreev (1988)	10	0.6	*Salix pulchra*	75
Dicrostonyx groenlandicus	Shelford (1943)	5	0.07	*Dryas* spp., *Salix* spp.	50
Lemmus lemmus	Framstad et al. (1993)	3.5	0.05	Poaceae, Cyperaceae	7
Myopus schisticolor	Eskelinen (1997)	3	0.03	Bryophyta (Poaceae)	15
Clethrionomys rufocanus	Krebs and Myers (1974)	4.8	0.04	*Vaccinium myrtillus*	15
Microtus agrestis	Myllymäki (1977)	3.3	0.03	Poaceae, Cyperaceae	7
Arvicola terrestris	Saucy et al. (1994)	6	0.15	*Trifolium pratense*	20
Ondatra zibethicus	Danell (1985)	4	1.4	Cyperaceae	7
Erethizon dorsatum	Spencer (1964)	32	5.5	*Pinus edulis, P. ponderosa*	450
Lepus americanus	Keith (1990)	10	1.5	*Betula* spp., *Salix* spp.	100
Alces alces	Messier (1991)	19	300	*Betula* spp., *Abies* spp.	210
Odocoileus virginianus	Fryxell et al. (1991)	24	100	*Quercus* spp., *Thuja* spp.	300
Ovis aries	Clutton-Brock et al. (1997)	3.5	40	Poaceae	7

Note: Plant longevity information is from Harper and White (1974).

or growth rate of its population. This pattern cannot be predicted by any other known hypothesis on population cycles than those involving plant defense, i.e., the grazing-induced plant-defence hypothesis and the mast-depression hypothesis (Selås et al. 2001).

The suggestion that a single factor, such as food, might explain most variation in multi-annual cyclicity may appear unrealistic. For example, it is hard to imagine that peak, but still relatively sparse, populations of cyclic grouse, feeding on very abundant plant species, could induce such strong and widespread defense reactions as required for a population crash. On the other hand, there are many herbivores, from mites and insects to birds and mammals that specialize on the same food plants. We believe that the combined grazing pressure from such a guild can mobilize a strong defense in plants, ultimately causing parallel cycles in all the herbivores specializing on that plant. By way of example, F. Schwerdtfeger's study on fluctuations in pine-eating moth populations over 46 years (in Varley 1949) show some co-variation ($K = 0.24$; $P < 0.001$) between four different species. Nevertheless, it is clear that other factors, such as predators (Krebs et al. 1995, Reid et al. 1995, Korpimäki and Norrdahl 1998) and parasites (Hudson et al. 1998) can also contribute to cyclic population fluctuations.

METHODS

To compare periodicity of cyclic animals and longevity of their food plants we needed information on both herbivore cycle length, species of food plants, and life span of these. Much data are available on herbivore cycle length but much less is known about relevant food plants and their longevity. Selection of data had

TABLE 2. Life history and cycle length of insect herbivores and longevity of their food plants.

Herbivore	Data source	Cycle length, median (yr)	Plant species	Plant longevity, mean (yr)
Strophingia ericae	Whittaker (1985)	6	*Calluna vulgaris*	25
Melolontha hippocastani	Schwerdtfeger (1968)	4.5	Poaceae	7
Lochmaea saturalis	Nielsen (1986)	6	*Calluna vulgaris*	25
Diprion pini	Geri (1988)	17	*Pinus sylvestris*	200
Neodiprion sertifep	Kangas (1963)	17	*Pinus sylvestris*	200
Pristiphora erichsonii	Jardon et al. (1994)	25	*Larix laricina*	180
Acleris variana	Morris (1959)	8	*Abies balsamea*	200
Choristoneura fumiferana	Royama (1984)	33	*Abies balsamea, Picea glauca*	250
Choristoneura occidentalis	Swetnam and Lynch (1993)	33	*Pseudotsuga menziesii, Abies concolor*	500
Choristoneura pinus	McCullough (2000)	9	*Pinus banksiana*	180
Zeiraphera diniana	Baltensweiler and Fischlin (1988)	9	*Larix decidua*	200
Bupalus piniarius	Varley (1949)	8	*Pinus sylvestris*	200
Epirrita autumnata	Tenow (1972)	9	*Betula verrucosa*	120
Malacosoma californicum	Myers (1988)	8	*Alnus rubra*	110
Coloradia pandora	Speer et al. (2001)	30	*Pinus ponderosa*	450
Hyloicus pinastri	Varley (1949)	13	*Pinus sylvestris*	200
Orygia pseudosugata	Myers (1988)	22	*Pseudotsuga menziesii*	600
Cerapteryx graminis	Danell and Ericson (1990)	7	Poaceae	7

Note: Plant longevity information is from Harper and White (1974).

to be based on knowledge of both these variables and also had to consider the risk of phylogenetic pseudoreplication, not only for the herbivores but also for the food plants. We restricted the analysis to monophagous animals or those feeding on a few plant species of similar longevity. Information on food plants and cycle length was usually from the same study, but in some cases, such as the microtines, muskrat (*Ondatra zibethicus*), snowshoe hare, moose, and white-tailed deer (*Odocoileus virginianus*), diet data were from other work in the same or nearby areas.

Further, because our hypothesis is based on responses of individual plants we considered only periodicities for local populations, unless there was synchrony in cycle dynamics over vast areas. For polyphagous vertebrate herbivores we considered only food plants of the limiting period of the year, i.e., winter for the species in Table 1. Difficulties in defining the limiting period for polyphagous grouse species forced us to omit these, despite the fact that many of them show distinct multi-annual cycles, often attributed to between-year variation in breeding success. If so, the relevant food could be that of the laying hen, the newly hatched chicks (often insects), older young, or a combination of these.

Finally, to avoid selection bias, most data on food-plant longevity were taken from the study by Harper and White (1974). As stressed by these authors their longevity data represent ''normally attainable age,'' best regarded as that at which dominant individuals die, i.e., when senility sets in. Length of the defense period is presumably related to such an age.

Choice of species and time period

Comparative analyses like our present study often are accused of being biased in favor of suitable species and/or time periods. We therefore discuss some important groups in terms of data selection:

Rodents.—To our knowledge, all long-term (>3 cycles) studies of cyclic small rodents (microtines) show short cycles (3–5 years). The microtine diet consists mainly of green plant parts, usually of graminoids and mosses. Typically, shoots of preferred grasses and mosses are shortlived, 5–10 and 15–20 yr, respectively (Harper and White 1974, Jonsdottir and Callaghan 1988, Økland 1995; E. Heegaard, *personal communication*). The exception to this general pattern is the collared lemming (*Dicrostonyx groenlandicus*), which often feeds on herbs and willows that attain ages of 50 years, but also to a large extent feeds on short-lived graminoids and mosses (Klein and Bay 1994).

To avoid pseudoreplication we give data for one species each in the microtine genera *Lemmus*, *Dicrostonyx*, *Myopus*, *Microtus*, and *Clethrionomys*. We stress that choice of species does little to change the overall picture of Fig. 1. In addition, we show data for water vole (*Arvicola terrestris*), muskrat, and porcupine (*Erethizon dorsatum*), all rodents. The porcupine data are based on dendrochronologic analysis and encompass three cycles.

Grouse.—In many tetraonid species chick survival/recruitment appears to be crucial for population density in the next breeding season (Moss and Watson 2001), but for Willow Grouse (*Lagopus lagopus*) in Siberia the proportion of adult birds breeding, varying between 38 and 100%, seems to be the factor determining population size (Andreev 1988). Winter and spring diets of these grouse are dominated by twigs and buds of a willow (*Salix pulchra*; Andreev 1988), a species often attaining an age of 75 years (K. Danell, *personal communication*). *Vaccinium* spp. and other shrub species figure prominently in the spring and summer diet of many tetraonids (Savory 1977, Spidsø 1980, De Franceschi and Boag 1991), suggesting an intermediate cycle length in these birds. However, since knowledge of the limiting period/diet in polyphagous grouse is inadequate (see above) we have omitted these species. In addition, most studied tetraonid populations have been subject to shooting, a factor Moss et al. (1996) found important in shaping, if not preventing, the multi-annual cycle in Red Grouse (*Lagopus scoticus*).

Ungulates.—We have included three species of ungulates in Table 1, two browsers with long between-peak periods (one and two cycles for white-tailed deer and moose, respectively) and one grazer, the Soay sheep, with a temporal pattern and diet similar to a microtine rodent. For white-tailed deer Turchin (2003) reported historical data covering a longer period with similar periodicity to that recorded by Fryxell et al. (1991). It appears that regular fluctuations occur only in northern deer populations, for which tree browse above the snow is the most important winter food. Caribou populations in the High Arctic appear to undergo extremely long (30–50 yr) oscillations (summarized in Caughley and Gunn [1993]). This fits well with the high longevity of their main winter food, lichen of the genus *Cladina*. Yet, these cycles may have less to do with induced resistance of food-plants than with sheer overgrazing, apparent from the lack of lichen in intensely grazed caribou winter pasture. This is one of the few herbivore–plant interactions often leading to dramatic food depletion. Usually, cyclic herbivore populations in the decrease phase are associated with only slight signs of overgrazing.

Insects.—Most long-time series are of pest species, in particular of moths feeding on forest trees. We have omitted some well-known forest pests such as *Lymantria* spp., *Hyphantria cunea*, and *Heterocampa guttivitta* that feed on a range of plant species of widely different longevity. On the other hand, we have included some closely related species that, in contrast to the rodents mentioned above, show no overlap in food plant choice.

Results and Discussion

Variation in life-span of food plants explains 72% of the variation in herbivore cycle length (Fig. 1). Cor-

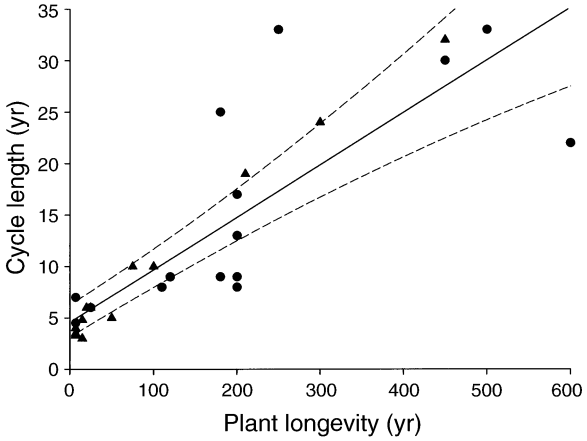

FIG. 1. Cycle length for herbivorous insects (●) and vertebrates (▲) in relation to food-plant longevity. Dashed lines show 95% confidence intervals calculated from 1000 resamples using bootstrapping techniques. The line is described by the equation $y = 0.05(x) + 4.58$ ($F_{1,30} = 77.6$, $n = 32$, $r^2 = 0.72$; $P < 0.001$ for both the F test and the r^2 correlation).

responding figures for vertebrates and insects are 99% and 56%, respectively. The lower value for insects may be due to the varying methods of documenting cycles in this group, adding to the variance in estimates of cycle length. Except for the porcupine, all periods of vertebrates were based on counts of individual animals, but for insects, period lengths were calculated from studies of tree-ring data, counts of individual insects, and the extent of damage on host plants, both on a local and regional scale. Also, some insect species with less clear cycles, e.g., *Orgyia pseudotsugata*, *Bupalus piniaria*, and *Pristiphora erichsonii*, may have become outliers because of difficulties in correctly estimating time periods between population peaks. Finally, most insects in Fig. 1 feed on trees, which often barely survive herbivore attacks (Jardon et al. 1994). Such morbidity, sometimes lasting for decades, paves the way for continuous insect attacks, possibly biasing records towards shorter cycle lengths.

The sample of cyclic animals in Fig. 1 is diverse, encompassing four orders of insects, four birds, and mammals up to the size of moose (*Alces alces*). Clearly, with sheep (*Ovis aries*) and Red Grouse (*Lagopus scoticus*) having short (3–6 yr) cycles and several insects extremely long (>30 yr) cycles, body mass contributes little in explaining cycle length across taxa. In a sample of vertebrates, path analysis shows that although 99% of the variation in cycle length is explained by the combined effects of herbivore body mass and food-plant longevity, only the latter factor contributes significantly and accounts alone for 92% of the variation in periodicity (Fig. 2).

The notion that populations of cyclic herbivores to a large extent are regulated by induced plant defense and consequently that cycle length is determined by plant longevity may help explain some general phenomena associated with population cycles. For example, older trees suffer higher mortality than younger ones during insect outbreaks, a fact compatible with the lower reproductive value of old trees, perhaps leading to a premature demobilization of their defense and increasing their vulnerability to renewed attacks by the herbivore. Generally, we would expect long-lasting outbreaks to induce a stronger and longer defense mobilization compared to shorter attacks. This appears to be the case in the tree-ring study (600 years) by Speer et al. (2001) on pandora moths defoliating ponderosa pine: out of 11 sites nine show a positive ($r = 0.15$, 0.28, 0.33, 0.44, 0.44, 0.50, 0.76, 0.86, and 0.94) and only two a negative ($r = -0.40$ and -0.47) correlation between duration of attack and interval to the next defoliation. Similarly, as pointed out by a reviewer, the severity of an attack should be reflected in a stronger response and a longer defense period. For example, the loss of bark and twigs could be considered more severe for a plant than the loss of annually renewed leaves/needles, and could result in longer cycles than expected. Indeed, Fig. 1 shows this to be the case with all the twig/bark-eating herbivores (the two grouse species, snowshoe hare, moose, white-tailed deer, and porcupine) being above the regression line. Also, the northwards increasing cycle length of microtines in Fennoscandia may be associated with a longer life-span of northern and alpine plants (Harper and White 1974) as compared with southern and lowland species.

Another prediction from this hypothesis is that herbivores feeding on the same plant species should show the same periodicity. This is clearly borne out by the three specialists on heather *Calluna vulgaris* (see Tables 1 and 2), which all have cycle lengths of six years despite differences in taxonomic affiliation (one bird, one beetle, one psyllid), size, and population growth rate. On the other hand, herbivorous insects on Scots pine *Pinus sylvestris* show a less constant period length, varying between 8 and 17 years.

Finally, different herbivore species in the same area may peak asynchronously depending on food-plant species in the diet. For example, Boutin et al. (1995) found snowshoe hares and voles to peak in different years and two lemming species, one eating herbs and willows and the other graminoids, showed asynchronous cycles locally (Pitelka and Batzli 1993). In con-

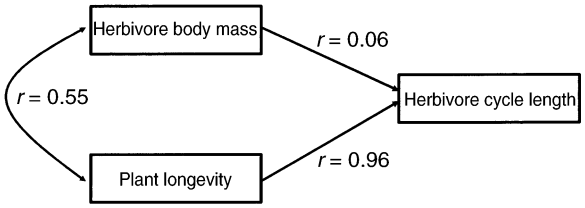

FIG. 2. A path diagram showing the joint effects of herbivore body mass and plant longevity on cycle length of herbivores; r values show the strength of the correlation.

trast, herbivores eating the same food plant should peak in parallel, irrespective of taxonomic relationships. Unfortunately, data are few except for some closely related species such as forest moths (see above), microtines (e.g., Framstad et al. 1993), and grouse (e.g., Lindström et al. 1997).

We conclude that data reviewed here are compatible with predictions from the hypothesis of herbivore-induced plant defense. This does not, however, mean that we exclude other factors as important in shaping cyclic dynamics. Experimental evidence for such effects has been reported for parasitism in red grouse (Hudson et al. 1998), predation in microtines (Korpimäki and Norrdahl 1998, Reid et al. 1995), and a combination of food and predation in snowshoe hares (Krebs et al. 1995). The latter study shows that both food and predation contributed to the cyclic pattern but their relative importance is difficult to evaluate.

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LITERATURE CITED

Andreev, A. 1988. The ten year cycle of the willow grouse of Lower Kolyma. Oecologia **76**:261–267.

Baltensweiler, W. 1985. On the extent and the mechanisms of the outbreaks of the larch budmoth (*Zeiraphera diniana* Gn., Lepidoptera, Tortricidae) and its impact on the subalpine larch–cembran pine ecosystem. Pages 215–219 *in* H. Turner and W. Tranquillini, editors. Establishment and tending of subalpine forest: research and management. Swiss Federal Institute of Forestry Research, Birmensdorf, Switzerland.

Baltensweiler, W., and A. Fischlin. 1988. The larch bud moth in the European Alps. Pages 331–351 *in* A. Berryman, editor. Dynamics of forest insect populations. Academic Press, New York, New York, USA.

Boutin, S., et al. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. Oikos **74**:69–80.

Bryant, J. P., I. Heitkonig, P. Kuropat, and N. Owen-Smith. 1991. Effects of servere defoliation on the long-term resistance to insect attack and leaf chemistry in six woody species of the southern African savanna. American Naturalist **137**:50–63.

Calder, W. A. 1983. An allometric approach to population cycles of mammals. Journal of Theoretical Biology **100**: 275–282.

Caughley, G., and A. Gunn. 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. Oikos **67**:47–55.

Clutton-Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. Maccoll, and S. D. Albon. 1997. Stability and instability in ungulate populations: an empirical analysis. American Naturalist **149**:195–219.

Danell, K. 1985. Population fluctuations of the muskrat in coastal northern Sweden. Acta Theriologica **30**:219–226.

Danell, K., and L. Ericson. 1990. Dynamic relations between the antler moth and meadow vegetation in northern Sweden. Ecology **71**:1068–1077.

De Franceschi, P. F., and D. A. Boag. 1991. Summer foraging by spruce grouse: implications for galliform food habits. Canadian Journal of Zoology **69**:1708–1711.

Eskelinen, O. 1997. On the population fluctuations and structure of the wood lemming *Myopus schisticolor*. International journal of Mammalian Biology **62**:293–302.

Framstad, E., N. C. Stenseth, and E. Østbye. 1993. Time series analysis of population fluctuations of *Lemmus lemmus*. Pages 97–115 *in* N. C. Stenseth and R. A. Ims, editors. The biology of lemmings. Academic Press, London, UK.

Fryxell, J. M., D. J. T. Hussell, A. B. Lambert, and P. C. Smith. 1991. Time lags and population fluctuations in white-tailed deer. Journal of Wildlife Management **55**:377–385.

Geri, C. 1988. The pine sawfly in central France. Pages 377–405 *in* A. Berryman, editor. Dynamics of forest insect populations. Academic Press, New York, New York, USA.

Ginzburg, L. R., and D. E. Tanneyhill. 1994. Population cycles of forest Lepidoptera: a maternal effect hypothesis. Journal of Animal Ecology **63**:79–92.

Ginzburg, L. R., and D. E. Tanneyhill. 1995. Population cycles: a critique of the maternal and allometric hypotheses. Journal of Animal Ecology **64**:290–293.

Harper, J. L., and J. White. 1974. The demography of plants. Annual Review of Ecology and Systematics **5**:419–463.

Haukioja, E., and T. Hakala. 1975. Herbivore cycles and periodic outbreaks. Formulation of a general hypothesis. Report from the Kevo Subarctic Research Station **12**:1–9.

Haukioja, E., and S. Neuvonen. 1987. Insect population dynamics and induction of plant resistance: the testing of hypotheses. Pages 411–432 *in* P. Barbosa and J. C. Schultz, editors. Insect outbreaks. Academic Press, San Diego, California, USA.

Hudson, P. J., A. P. Dobson, and D. Newborn. 1998. Prevention of population cycles by parasite removal. Science **282**:2256–2258.

Jardon, Y., L. Filion, and C. Cloutier. 1994. Long-term impact of insect defoliation on growth and mortality of eastern larch in boreal Quèbec. Ecoscience **1**:231–238.

Jonsdottir, I. S., and T. V. Callaghan. 1988. Interralationships between different generations of interconnected tillers in *Carex bigelowii*. Oikos **52**:120–128.

Kangas, V. E. 1963. Über das schädliche Auftreten der *Diprion*- Arten (Hym., Diprionidae) in finnischen Kifernbeständen in diesem Jahrhundert. Zeitschrift für Angewandte Entomologie **5**:188–194.

Karban, R., and I. T. Baldwin. 1997. Induced responses to herbivory. University of Chicago Press, Chicago, Illinois, USA.

Keith, L. B. 1990. Dynamics of snowshoe hare populations. Pages 119–195 *in* H. H. Genoways, editor. Current mammalogy. Plenum press, New York, New York, USA.

Klein, D. R., and C. Bay. 1994. Resource partitioning by mammalian herbivores in the high Arctic. Oecologia **97**: 439–450.

Korpimäki, E., and K. Norrdahl. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. Ecology **79**:2448–2455.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science **269**:1112–1115.

Krebs, C. J., and J. H. Myers. 1974. Population cycles in small mammals. Advances in Ecological Research **8**:267–299.

Krukonis, G., and W. M. Schaffer. 1991. Population cycles in mammals and birds: does periodicity scale with body size? Journal of Theoretical Biology **148**:469–493.

Lindström, J., E. Ranta, M. Lindén, and H. Lindén. 1997. Reproductive output, population structure and cyclic dynamics in Capercaillie, Black Grouse, and Hazel Grouse. Journal of Avian Biology **28**:1–8.

May, R. M. 1981. Theoretical ecology. Blackwell, Oxford, UK.

McCullough, D. G. 2000. A review of factors affecting the population dynamics of jack pine budworm (*Choristoneura pinus pinus* Freeman). Population Ecology **42**:243–256.

Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. Journal of Animal Ecology **60**:377–393.
Morris, R. F. 1959. Single-factor analysis in population dynamics. Ecology **40**:580–588.
Moss, R., and A. Watson. 2001. Population cycles in birds of the grouse family (Tetraonidae). Advances in Ecological Research **32**:53–111.
Moss, R., A. Watson, and R. Parr. 1996. Experimental prevention of a population cycle in red grouse. Ecology **77**: 1512–1530.
Myers, J. 1988. Can a general hypothesis explain population cycles of forest Lepidoptera? Advances in Ecological Research **18**:179–242.
Myllymäki, A. 1977. Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. Oikos **29**:468–493.
Nielsen, B. O. 1986. Masseangreb af lyngens bladbille (*Lochmaea saturalis* Thoms.) på danske lyngheder 1900–1984 (Coleoptera: Chrysomelidae). Entomologiske Meddelelser **53**:99–109.
Økland, R. H. 1995. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. Journal of Ecology **83**:697–712.
Peterson, R. O., R. E. Page, and K. M. Dodge. 1984. Wolves, moose, and the allometry of population cycles. Science **224**:1350–1352.
Pitelka, F., and G. O. Batzli. 1993. Distribution, abundance, and habitat use by lemmings on the north slope of Alaska. Pages 213–236 *in* N. C. Stenseth and R. A. Ims, editors. The biology of lemmings. Academic Press, London, UK.
Reid, D. G., C. J. Krebs, and A. Kenney. 1995. Limitation of collared lemming population growth at low densities by predation mortality. Oikos **73**:387–398.
Rhoades, D. F. 1985. Offensive–defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. American Naturalist **126**:181–195.
Royama, T. 1984. Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. Ecological Monographs **54**:429–462.
Saucy, F. 1994. Density-dependence in time-series of the fossorial form of the water vole, *Arvicola terrestris*. Oikos **71**: 381–392.
Savory, C. J. 1977. The food of red grouse chicks *Lagopus l. scoticus*. Ibis **119**:1–9.
Schwerdtfeger, F. 1968. Ökologie der Tiere. Paul Parey, Hamburg, Germany.
Selås, V., G. A. Sonerud, T. Histol, and O. Hjeljord. 2001. Synchrony in short-term fluctuations of moose calf body mass and bank vole population density supports the mast depression hypothesis. Oikos **92**:271–278.
Shelford, V. E. 1943. The abundance of the collared lemming (*Dicrostonyx groenlandicus* (Tr.) var *richardsoni* mer) in the Churchill area 1929 to 1940. Ecology **24**:427–484.
Speer, J. H., T. W. Swetnam, B. E. Wickman, and A. Youngblood. 2001. Changes in pandora moth outbreak dynamics during the past 622 years. Ecology **82**:679–697.
Spencer, D. A. 1964. Porcupine populations fluctuations in past centuries. Journal of Applied Ecology **1**:127–149.
Spidsø, T. K. 1980. Food selection by willow grouse *Lagopus lagopus* chicks in northern Norway. Ornis Scandinavica **11**: 99–105.
Swetnam, T. W., and A. M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. Ecological Monographs **63**:399–424.
Tenow, O. 1972. The outbreak of *Oporina autumnata* Bhk. and *Operophthera* spp. in the Scandinavian mountain chain and northern Finland. Zoologiska Bidrag från Uppsala **2**(Supplement):1–107.
Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press, Princeton, New Jersey, USA.
Underwood, N. 1999. The influence of plant and herbivore characteristics on the interaction between induced resistance and herbivore population dynamics. American Naturalist **153**:282–294.
Varley, G. C. 1949. Population changes in German forest pests. Journal of Animal Ecology **18**:117–122.
Watson, A., and R. Moss. 1979. Population cycles in the Tetraonidae. Ornis Fennica **56**:87–109.
Whittaker, J. B. 1985. Population cycles over a 16-year period in an upland race of *Strophingia ericae* (Homoptera: Psylloidea) on *Calluna vulgaris*. Journal of Animal Ecology **54**:311–321.